Distribution of a Herring Fishery Relative to Submerged Vegetation, Herring Spawn Distribution and Oceanographic Factors

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DISTRIBUTION OF A HERRING FISHERY RELATIVE TO SUBMERGED VEGETATION, HERRING SPAWN DISTRIBUTION AND OCEANOGRAPHIC FACTORS

by

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ABSTRACT

Hay, D. E., C. D. Levings, and M. J. Haney. 1984. Distribution of a herring fishery relative to submerged vegetation, herring spawn distribution and oceanographic factors. Can. MS Rep. Fish. Aquat. Sci. 1760: 53 p.

The distribution of herring gillnets was recorded by aerial photography of a commercial herring fishery during March 4-6, 1981 in Lambert Channel. The gear and vessel distribution was plotted over previously determined distributions of submerged vegetation and the 1981 spawn distribution. Most spawning occurred after the fishery closure. Most vessels and gillents were not positioned over vegetation that was eventually used for spawn deposition. SCUBA diver surveys found no evidence of physical damage to the vegetation. Dead fish, killed but not captured by the fishery, were not substantial and did not cause any detectable deleterious effect on water quality. No evidence was found to substantiate concerns that the roe fishery was causing a qualitative degradation or "souring" of herring spawning grounds.

Key words: herring, spawning grounds, oceanographic factors, nutrients, dissolved oxygen

RÉSUMÉ

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Du 4 au 6 mars 1981, on a relevé la distribution des filets maillants utilisés pour la pêche commerciale du hareng dans le chenal Lambe à l'aide de photographies aériennes. La position des engins et des bateaux a été rapportée sur les répartitions prédéterminées de la végétation submergée et la répartition du frai de 1981. La plus grande partie de la fraie a eu lieu après la fermeture de la pêche et la plupart des filets millants et des bateaux ne se trouvaient pas dans les zones de végétation où le frai a été finalement déposé. Des levés menés par des plongeurs n'ont pas révélé de dommages physiques à la végétation. Les poissons morts, tués mais non capturés par les pêcheurs, n'étaient pas nombreux et ne causaient pas d'incidence négative décelable sur la qualité de l'eau. On n'a découvert aucune preuve à l'appui des préoccupations selon lesquelles la pêche de la rogue entraînait une dégradation qualitative ou ferait "surir" les frayères du hareng.

Mots-clés: hareng, frayères, facteurs océanographiques, bioéléments, oxygène dissous

INTRODUCTION

The British Columbia sac-roe herring fishery began in the early 1970s. Since that time there have been concerns, both within industry and government, that the fishery might have deleterious impacts on the stocks or on their spawning habitats. These impacts have not been clearly defined although they relate to suspicions that the gillnets might be uprooting and destroying submerged vegetation used as spawning substrate. Another concern involves the assumption that there is a substantial drop-out associated with gillnets so that large numbers of dead fish are deposited on the fishing and spawning grounds during and after fishing operations. If true, then the carcasses could have a deleterious impact on the developing herring eggs. However, a more general concern is that, as a consequence of dead fish left on the bottom, the biological suitability of the spawning area might be permanently altered - or 'soured'.

This report addresses these questions and ties together the results of several independent but coordinated studies that occurred before, during and after the herring spawning and fishery in Lambert Channel in March, 1981. Quantitative estimates of the gillnet fleet size (including associated vessels) and their distribution during the two days of the fishery is documented using aerial photographic analysis. This fleet distribution is shown relative to the distribution of submerged vegetation and spawn. Measurements of salinity, temperature, and water quality throughout the area were made to determine if there were detectable changes in water quality. Finally, SCUBA divers quantified the numbers of dead herring on the bottom and noted their elimination by scavengers.

1. DISTRIBUTION AND CONCENTRATION OF VESSELS AND GEAR

Aerial surveys of the Lambert Channel fisheries in the Strait of Georgia were made to determine the proportion of gear that was fished directly over spawning areas. High resolution black and white infrared film was used to photograph the seine fishery of March 4, and the gillnet openings of March 5 and 6. The location of gillnets was determined from identification of buoys attached to the nets. On March 4, vessels were distributed from Cape Lazo in the north west to Lambert Channel, south of Shingle Spit in the south (Fig. 1). Seiners were mainly in the northern half of this area but gillnet vessels and packers were spread throughout. Most gillnetters were anticipating an imminent gillnet opening and were either scouting for fish or taking a potential fishing position.

The first opening for gillnets lasted from 1800 PST March 4 to 1700 PST March 5 for a total of 23 hours. The concentration of gillnet vessels increased during the evening of March 4 and reached a maximum in the afternoon of March 5. Figure 2 shows an overview of aerial photographs of the vessel and gillnet gear distribution for the morning (1030 PST) of March 5. Most vessels and gear were concentrated in the vicinity of the north end of Denman Island and Sandy Islands. There were also vessels distributed fairly

uniformly to the south in Lambert Channel-to an area south of Fillongly Park. A relatively small number of boats set their gear in the vicinity of Shingle Spit on Hornby Island.

The approximate distributions of (1) gillnets, as indicated by the buoys (2) the gillnet punts and (3) the gillnet support vessels is indicated in Fig. 2 by different symbols. The gillnets were closest to the shore and gillnet support vessels were farthest away from the shore. Gillnet punts we generally in between. The orientation of gillnets in this region was generally parallel to the shore. This is shown by occasional lines joining two open circles. To avoid over-crowding, each open circle actually represents pairs or two buoys. Also, sometimes buoys were too close together to show distinctly at this scale and consequently all pairs are not shown and total gear is slightly underestimated in this figure. Support vessels consisted mainly of small fishing boats-trollers, salmon gillnetters, etc.-that served as accommodation to gillnet fishermen. Packing vessels and patrol vessels are also included in this group. These boats were mainly anchored in deeper water, well outside of the vicinity of submerged vegetation and fishing activity.

The gillnet punts, used to haul and shake the gillnets, were distributed between the gear and the support boats. However their distribution varied with time. They were either directly over the gear when hauling nets, in transit or tied up to the support vessels. A small number of gillnet punts are self-contained or operate without a support vessel and use shore-based support. They use accommodation ashore, usually trucks or campers, in between hauling nets. Perhaps it was these punts that worked the southern edge of the fishing locations where road access was close.

The distribution of gear was different on the second day-March 6. The gillnet opening then extended from 0900 to 1500 PST. Aerial photographic analysis of fleet distribution during this opening is shown in Figure 3. The main differences between this distribution and that of the previous day are (1) the fishing gear moved closer to shore and (2) the fleet was divided, roughly, into 4 areas: (1) North Denman-Sandy Island; (2) North of Fillongly Park; (3) a small area about 2 km south of Fillongly Park and (4) Shingle Spit, Hornby Island. The likely explanations for this shift in gear and vessel distribution are (1) the fishermen were following the active spawning areas which became concentrated in several areas on the evening of March 5 and morning of the 6th; (2) the total fleet size was reduced on the second day so the distribution of the fishing gear was reduced.

The photographic analyses show a total of 486 punts and 1,133 buoys present on March 5. Assuming that there are two buoys per net, the total number of nets would then be 566 - so that there were 80 more nets than punts. This discrepancy between the punts and nets could be explained by some error in photo interpretation because sometimes individual buoys are difficult to resolve. Also some nets might have been fished with 3 or more buoys. However, it is also possible that there were some unauthorized nets being fished in the area because there were only 501 gillnets licensed to fish in the Strait of Georgia (Chalmers et al. 1982). On March 6, the number of punts declined to 335 and the number of buoys to 709 or 354 nets for a discrepancy of 19 more punts then estimated nets.

The first opening for gillnets on March 4-5 lasted for 23 hours; the second on March 6 lasted for 6 hours. Assuming the number of punts on March 4-5 was 486, this represents a total of 11,178 fishing hours during the first opening and 2010 fishing hours during the second opening for a total of about 13,200 hours of fishing. With a total gillnet catch of approximately 7000 tons (Chalmers et al. 1982), this corresponds to a catch rate of 0.5303 tons per hour per punt. Punts fishing the full 29 hours would have caught an average of about 15 tons during the opening.

2. THE DISTRIBUTION OF GILLNETS, SPAWN AND VEGETATION

To determine the distribution of gillnets relative to vegetation we transposed detailed aerial photographs of the gillnet buoy distribution to charts of submerged vegetation distribution for the Lambert Channel area in 1979 (Haegele and Hamey 1981). It is possible that some annual changes in vegetation distribution and density could occur between 1979 (the year of the vegetation survey) and 1981 (the year of the gillnet survey) but major changes are unlikely (Haegele and Hamey 1980). The location of gillnet buoys in 1981 was plotted relative to the vegetation distribution in 1979 (Figs. 4-13). The inner and outer margins of the 1981 spawn distribution were identified by divers (Haegele 1982).

(i) Sandy Island: March 5-6

The detailed distribution of buoys on March 5 and 6 are shown in Figures 4 and 5 respectively. On March 5 much of the gear was outside the vegetation zone-in water between 3 and 5 fathoms. The remainder was in shallower water-at 1030 PST, (the time of the aerial photograph) and distributed over areas occupied by red and brown algae.

Vertical lines show the distribution of spawn in terms of the inner and outer margins. These limits were determined by SCUBA diver surveys (Haegele 1982). The distribution of gear was on the outer edge of the spawn distribution on both days. The gear was closer to shore on March 6, but most buoys were outside areas occupied by spawn. In fact, no spawn was present in the area on March 5: the water was clear, without milt. However, heavy spawning activity started on March 6 and the water was very cloudy with milt at the time of the closure at 1500 PST, March 6.

(ii) North Denman Island: March 5-6

There was a reduction in the amount of gear between March 5 (Fig. 6) and March 6 (Fig. 7). (The north western margin overlaps the adjacent figures by more than 1 km.) The gillnets in this region were mainly over the outer edges of vegetation and over substrate classifed as bare:mainly sand, mud cobble etc. The dark vertical lines indicating spawn distribution are shown over one location classified as 'bare'. Ordinarily, herring spawn is not found over bare substrate and it is likely that some of these bare areas had small 'patches' of vegetation on which spawn occurred. These patches are

probably sparse so that from the overview of an aerial photograph, the location was described as bare. From the perspective of a SCUBA diver, however, the outer limit of spawn would be the outermost patch on which spawn occurs, even if there is a lot of bare substrate between that patch and shore.

(iii) Komas Bluff

There was also a sharp decline in the number of buoys and an inshor. movement of gear between March 5 (Fig. 8) and March 6 (Fig. 9). On March 5, most of the nets, in the vicinity of Komos Bluff, were either outside the vegetation zone or on its outer margins. Spawn was deposited mainly after the March 6 fishing closure, inside the fished area.

(iv) Fillongly Park vicinity

On March 5, gillnets were distributed so that about one-half were on vegetated areas, and the other half on bare areas (Fig. 10). On March 6 the gear was closer to shore and most was over vegetated areas (Fig. 11). Spawning was remained light or negligible during the two days of the gillnet fishery, but its subsequent distribution was largely inside of the March 5 gillnet distribution. On March 6, however, the gear was distributed over areas later used heavily for spawning.

There were only a few nets in the southeastern section Fillongly Park (i.e. the middle of Figs. 10-11). The vegetation zone here is narrow and most nets were either over bare substrate or the outer edges of vegetation.

(v) Hornby Island

On March 5 (Fig. 12) the distribution of nets was completely over bare substrate. On March 6 the gear moved closer to shore and about half was over the outer vegetation zones (Fig. 13). There was no significant quantity of spawn recorded for this location, although a narrow band of spawn is shown across the channel on Whalebone Point, Denman Island.

(vi) Summary of gear, vegetation and spawn distribution

The gillnets were further from shore on March 5 than March 6. On March 5, approximately 56% were fishing was over submerged vegetation; 44% were over bare substate. The fleet and gear moved closer inshore during the second (March 6) opening and 81% was over submerged vegetation. For the entire opening, a total of about 5500 hours or 39% was spent fishing over bare substrate; the remainder, or 61% was spent fishing over vegetation. The spawn distribution did not extend to the full width of the vegetation zone, so most of the gillnet fishing activity occurred over areas that were offshore from the areas used for spawning. The diving transects (Figs. 4-13) do not have sufficient detail to allow an estimate. Probably the overlap between spawn areas and fishing is less than 50%. If the gillnet fishing area were

estimated relative to the area covered by spawn or vegetation in the region as a whole (i.e. statistical area 14, or even Georgia Strait), then the proportion of the region covered by gillnets would be very small. The significance of this is that we cannot provide any quantitative evidence that herring gillnets do or do not have deleterious impacts on the bottom vegetation, or spawn. However, even if they did, such impacts would be confined to a small proportion of the total spawning area.

Divers conducting herring spawn surveys have not observed any appreciable damage to vegetation after gillnet fisheries. Uprooted vegetation or fragments are generally washed ashore following strong winds, particularly from the south-east (Hay and Miller 1982). Uprooted vegetation is usually seen, both in the water and along the shore. Often piles or 'windrows' of vegetation can be seen in March and April at many points along the eastern shores of Vancouver Island. However, very few of these areas are fished by gillnets. Extensive broken or uprooted vegetation in the water or on the beach was not seen after the 1981 gillnet fishery in Lambert Channel. Therefore, our conclusion is that gillnets did not result in widespread vegetation damage in the 1981 Lambert Channel fishery.

3. DISTRIBUTION OF WATER CHARACTERISTICS WITH RESPECT TO SPAWN

Transects positions (Fig. 14) were established to study oceanographic factors before, during, and after spawning, and tabulated data are presented elsewhere (Seakem 1981). Spawn abundance data from diver surveys (Haegele 1982) were compared with the temperature and salinity conditions from Transects A and B (Fig. 15a,b) to evaluate environmental conditions where eggs were incubating. On March 8, herring spawn near transect A was exposed to temperatures between 8.1 and 8.3°C and salinities from 26.2 to 27.7°/‥. Temperatures and salinities later on (March 26 and April 21) were higher, ranging from 9.0-9.4°C and 27.8-28.4°/‥. Salinities on Transect B were slightly higher, ranging from 27.5 to 28.8°/‥, but temperatures were very similar to those from Transect A and showed the same pattern of increase in temperatures. Figure 16 shows a representative vertical profile of properties from the western part (Transect B, Station 4) of the study area where because surface waters were more brackish stratification of properties was evident. Wind and tidal action could lead to mixing of lower salinity water onto spawn in this area. Further into Lambert Channel, on transects D and E, there was very little evidence of stratification.

The distribution of surface salinity in the study area on four samples dates, before and after spawning, is shown on Figure 17a-d. As shown surface salinities were lower and more variable at the westerly transects. Herring spawning was heaviest in this area. Herring spawning was more intensive at the westerly transects where lower salinities were recorded. The brackish water in these areas may have resulted from the discharge of the Courtenay River, whose estuary is at the northwest end of Denman Island. Inshore of certain transects, especially B and C, fresh water seeps were noted on the beaches and these may have lowered salinities on an extremely local scale. Salinities on the southeast transects were in the upper range of

values reported by Outram (1975) for herring spawning sites on the western side of the Strait of Georgia, namely 22.4°/.. to 28.7°/.. A correlation between freshwater seeps and herring spawning was also suggested by Rabin (1977) for Humboldt Bay, California. Laboratory experiments conducted by Alderdice and Velsen (1971) showed that maximum percent viable hatch, larval size at hatching, and maximum survival to yolk sac absorption occurred in a trial at 16.41°/.. salinity and 6.85°C. Ginzberg (1968) noted that herring sperm motility persists longer in lower salinity water and thus brackish water may be an advantage for fertilizing eggs.

Nutrients and Dissolved Oxygen

In a heavy concentration of spawn on March 7, phosphate and ammonia showed a peak in concentration at about 1 m (Fig. 18). Nitrate appeared to be uniformly distributed through the water column (Fig. 18). Ammonia values at 5 m depth over transect B, an area where about 500 dead herring were placed, and a site close to an abandoned net with about 1000 fish were compared. In 5 samples there was little variation with a mean value of 0.044 mg L^{-1} and range 0.036 to 0.055 mg L^{-1}.

Surface levels of phosphate and nitrate were enhanced during the time when "white water" overlay the spawning ground. Total phosphate values rose after spawning began on March 6, increasing from approximately 0.08 mg L^{-1} on March 4 to about 0.21 mg L^{-1} on March 8 (Fig. 19). By March 12, total phosphate levels had decreased to approximately 0.10 mg L^{-1}. Nitrate levels showed a similar pattern, peaking at about 0.42 mg L^{-1} (Fig. 20). Prespawning concentrations of nitrate and phosphate were similar to values reported by Stockner et al. (unpublished data) at a station east of Hornby Island in March 1977.

Dissolved oxygen (D.O.) values at 3 and 5 m, near bottom, were compared at the area of the dumped fish (station D5; Fig. 14) and the abandoned net (station AN; Fig. 14) (9 samples) with data from adjacent transects obtained on the same day (11 samples). As judged by a t-test (Steel and Torrie 1960), there was no significant difference ($p>0.05$) between D.O. values at the locations (mean values 8.66 mg L^{-1} vs 7.43 mg L^{-1} respectively; approximately 80% saturation). Samples obtained in heavy spawn (Transect B, March 8) were lower than expected (34.9 to 69.9% saturation in 12 samples at depths 1 to 15 m), probably because of the biological oxygen demand of the gametes and associated bacteria.

There was therefore little evidence of decreased water quality even when moderate numbers of dead fish were aggregated to simulate a gillnet dropout situation. If large scale effects were occurring, decreased D.O. levels and increased concentrations of nutrients in bottom waters near the dead fish should have been observed. Conditions might be expected to resemble those in coastal waters where fish plant wastes are dumped (e.g., Dale and Dawson 1975; Champ et al. 1981). If a loaded seine or a completely saturated gillnet were disposed of in shallow water, significantly greater impacts might be expected. However there are no quantitative data available on such situations.

Predator attraction might be considered another index of impact. For example Humphreys (1975) reported that sunstars (Pycnopodia spp.) were observed eating dead herring that had fallen from gillnets in a Barkley Sound fishery. However at Denman Island very few large predators were observed by divers in this study. A few herring carcasses collected from the bottom were examined in the laboratory for smaller crustaceans which had been attracted to the fish. Only about 10 specimens, amphipods of the family Photidae, were observed on these fish. This was far fewer than expected and less than commonly attracted to herring used as crab bait.

In summary there was little evidence of the degraded water quality or other effects such as predator attraction. Gillnet fallout of herring had a minimal effect on the local benthic environment of the Denman Island spawning ground.

2. DISCUSSION AND CONCLUSION

Judging by the 1981 Lambert Channel fishery there is no evidence that the herring gillnet fishery had any deleterious effects on submerged vegetation or on water quality.

Some herring are killed and fall to the bottom during a gillnet fishery, but estimates of totals are relatively small.

Total dropout in the Lambert Channel Fishery was estimated at 0.118 fish per M^2-for a total estimated dropout in the fishery about 93 tons (Hay et al. 1981). This corresponds to an uncaptured mortality-or wastage of 1.7%. Another estimate made for the 1983 Lambert Channel Fishery was a total wastage of 80 tons from a total catch of approximately 8500 tons-Or 0.9% (Haegele, unpub. data). This 1983 estimate corroborates the 1981 estimate and indicates a very low rate of wastage. It is likely that wastage rates associated with other gear and other fisheries, particularly the discards in trawl fisheries or the shaker mortalities of troll fisheries are much higher. These fisheries, however, are not often as geographically concentrated as the herring gillnet fishery. The estimated densities of dead herring on the bottom, following a fishery, are roughly 1 per 10 m^2. This dead fish density would be seen, only over that area of spawn deposition over which fishing occurred. In the 1981 Lambert Channel Fishery this would be, roughly, 50% or less of the total area of spawn deposition. When dead herring are deposited in the midst of spawn, there is no observable effect on the surrounding eggs. Most dead fish fall to the bottom, on sand or mud, between the vegetation patches or the bases of individual plants and are not in direct contact with eggs which are attached to buoyant vegetation above. Unless the vegetation has a very low height, such as rockweed (Fucus) the possibility for actual contact between a dead herring and herring eggs is limited. In the instance of Fucus, it is mainly intertidal where little or no fishery occurs. Also bird and other scavengers usually rapidly remove accessible herring carcasses. Similar scavenger removal must occur underwater. Dead fish abundance was monitored on the bottom of Lambert Channel after the 1981 fishery and over 90% had disappeared within 20 days (Hay et al. 1982). However, no obvious underwater scavenger or predator attraction was observed

during this work, but, predators or scavengers could be most active at night. Also some carcasses could be removed by strong currents or be buried by shifting bottom sediments. Microbial decomposition could accompany these processes. The concentration of dead fish that we observed is not likely to have any effect on water quality particularly when no detectable effects could be seen in the vicinity of dead herring that were artificially concentrated at very much higher densities than those normally observed.

Finally, water chemistry is markedly changed during a spawning, bu this is a natural change associated with a massive input of organic material associated with herring sex products: eggs and milt. The increase in nitrate and phosphate (Fig. 19) may lead to localized increases in production of bacteria and phytoplankton, but further data are required to investigate this possibility. The magnitude of this material is enormous: by weight it should amount to about 25% of the total tonnage of spawning herring. This represents the approximate relative weight of herring and ovaries. Hay and Fulton (1983) speculate that this intense concentration of herring sex products could promote secondary production, particularly in the form of eggs of zooplankton which would serve as a food supply for herring larvae. In contrast to this natural organic input from spawning, the effect of a relatively small number of dead herring is insignificant.

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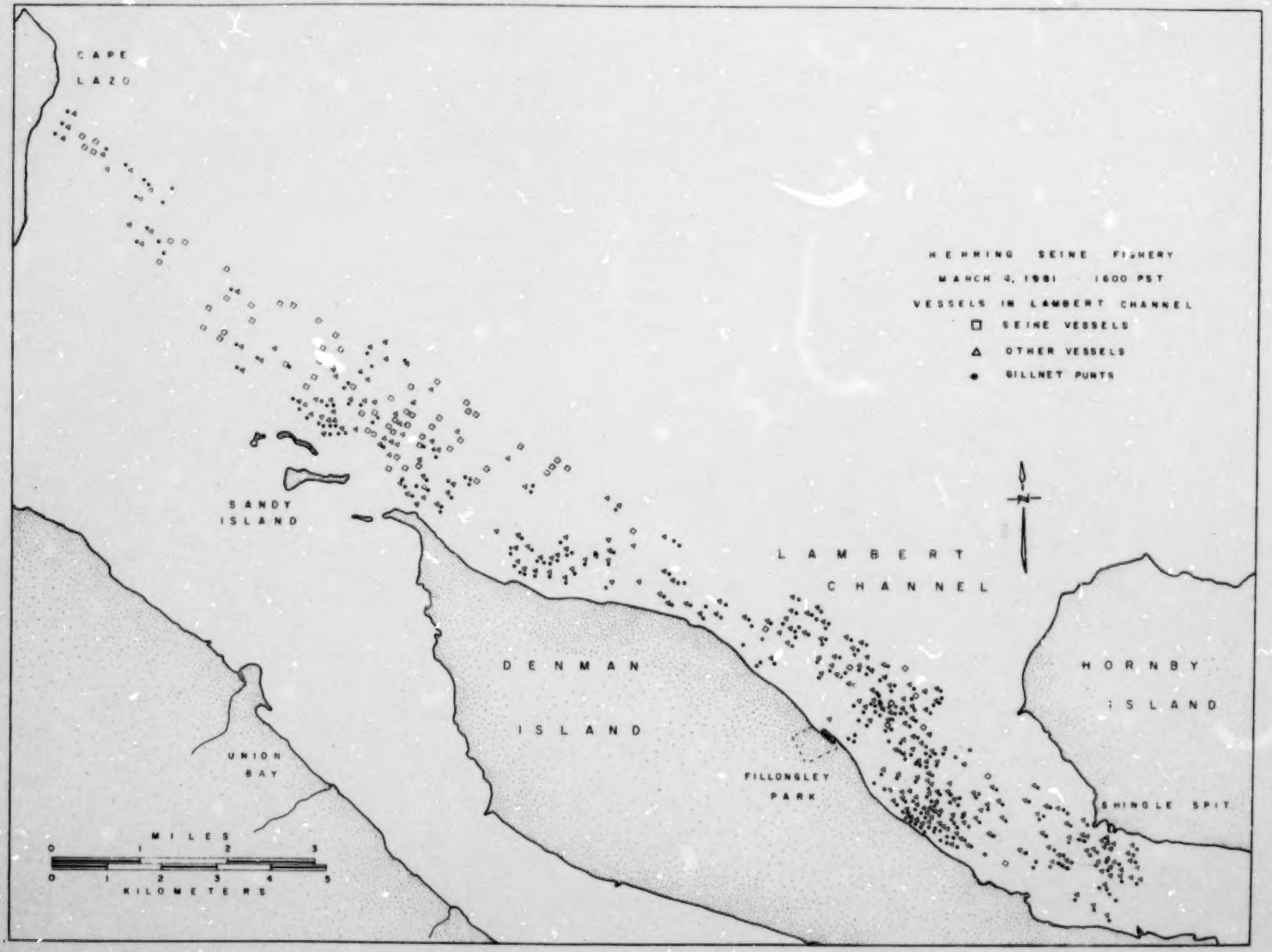


Figure 1. An overview of the distribution of vessels on March 4, 1981 during a fishery opening for seines. Most seiners were located in the northwest half of the area. Gillnetters were distributed throughout, but the main concentration was south of Fillongly Park.

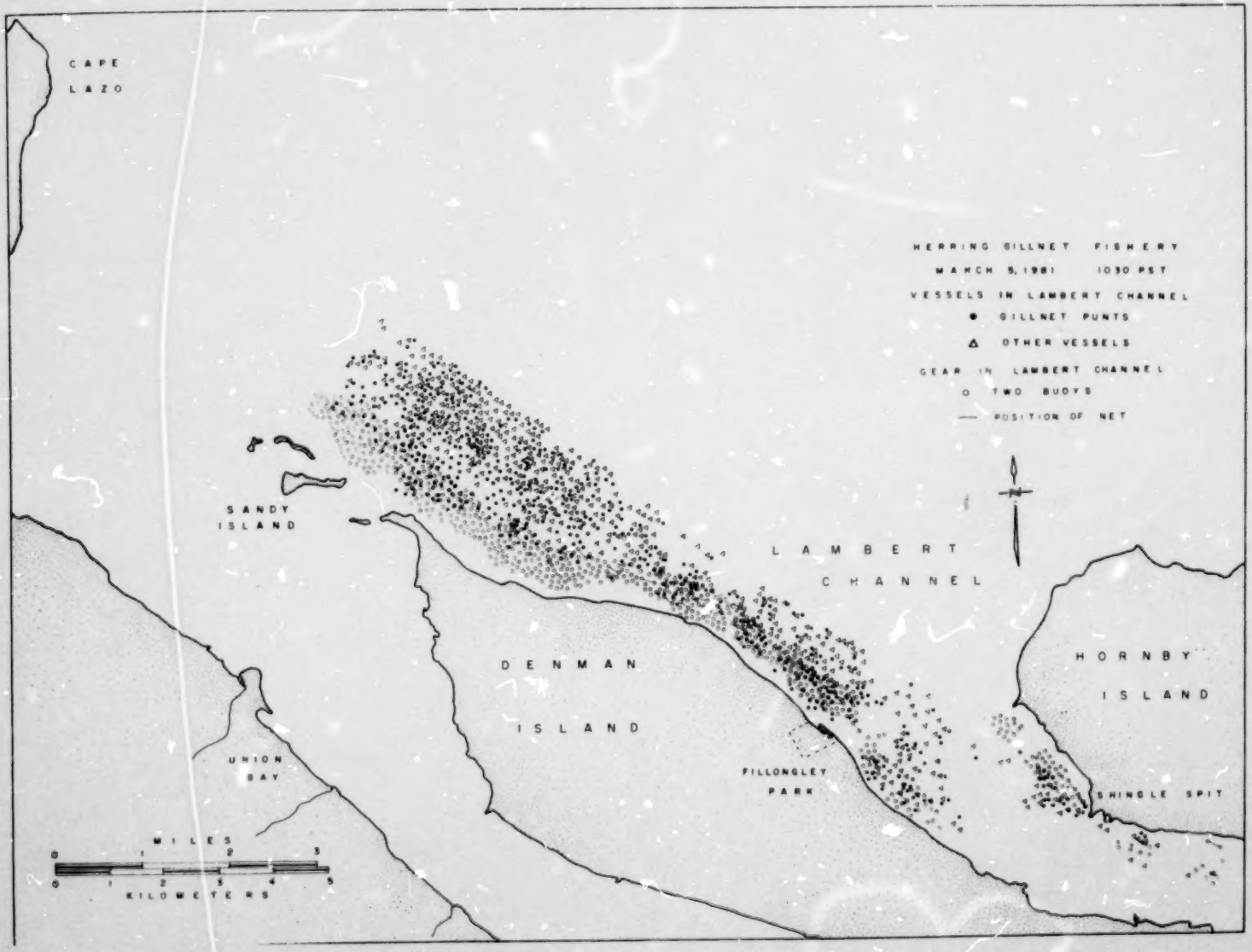


Figure 2. An overview of the distribution of vessels and gillnets on March 5, 1982, during the first day of a herring roe fishery opening for gillnets. See text for detailed explanation.

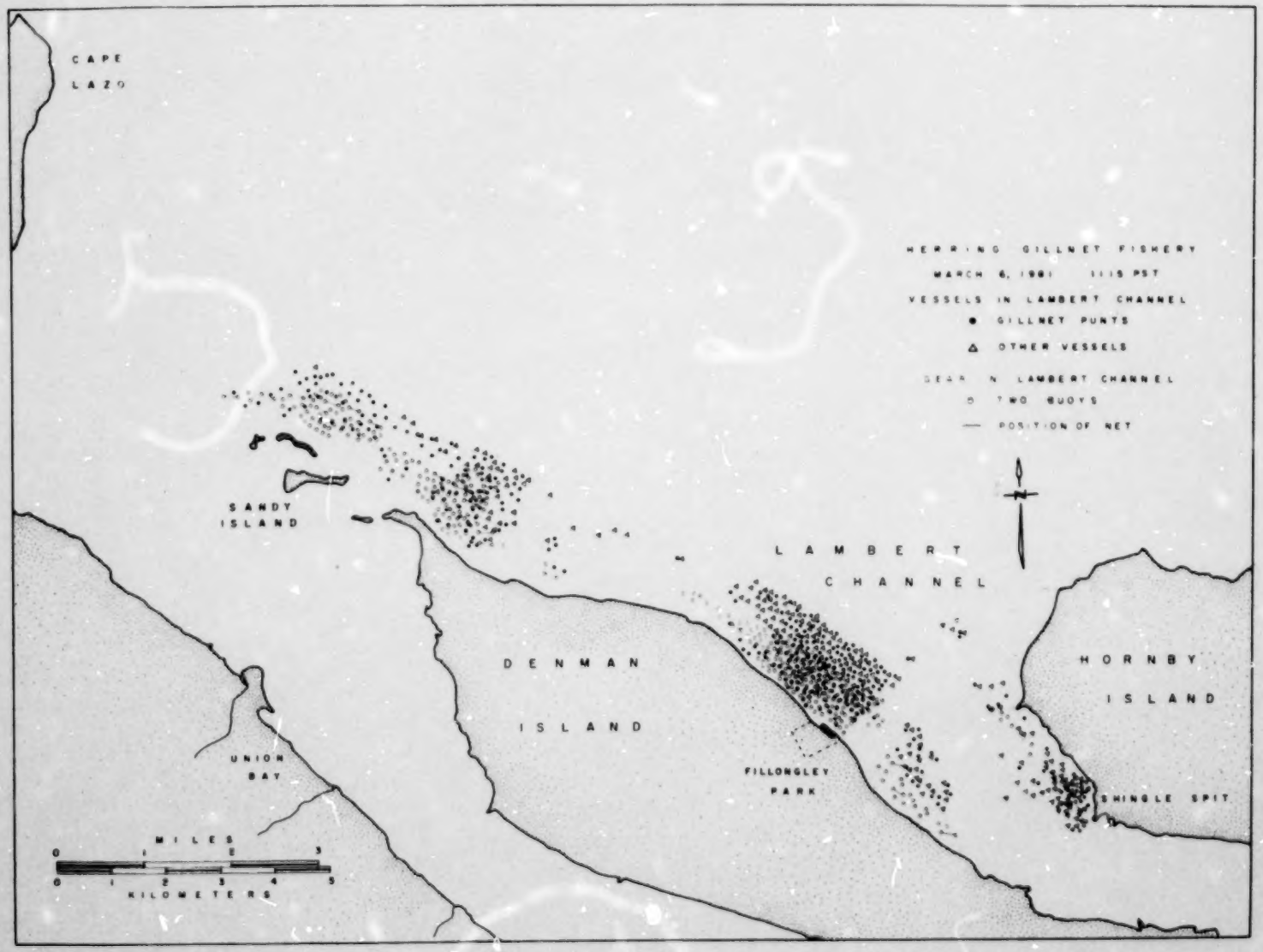


Figure 3. An overview of the distribution of vessels and gillnets on March 6, 1982 during the second day of a herring roe gillnet opening. See text for detailed explanation.

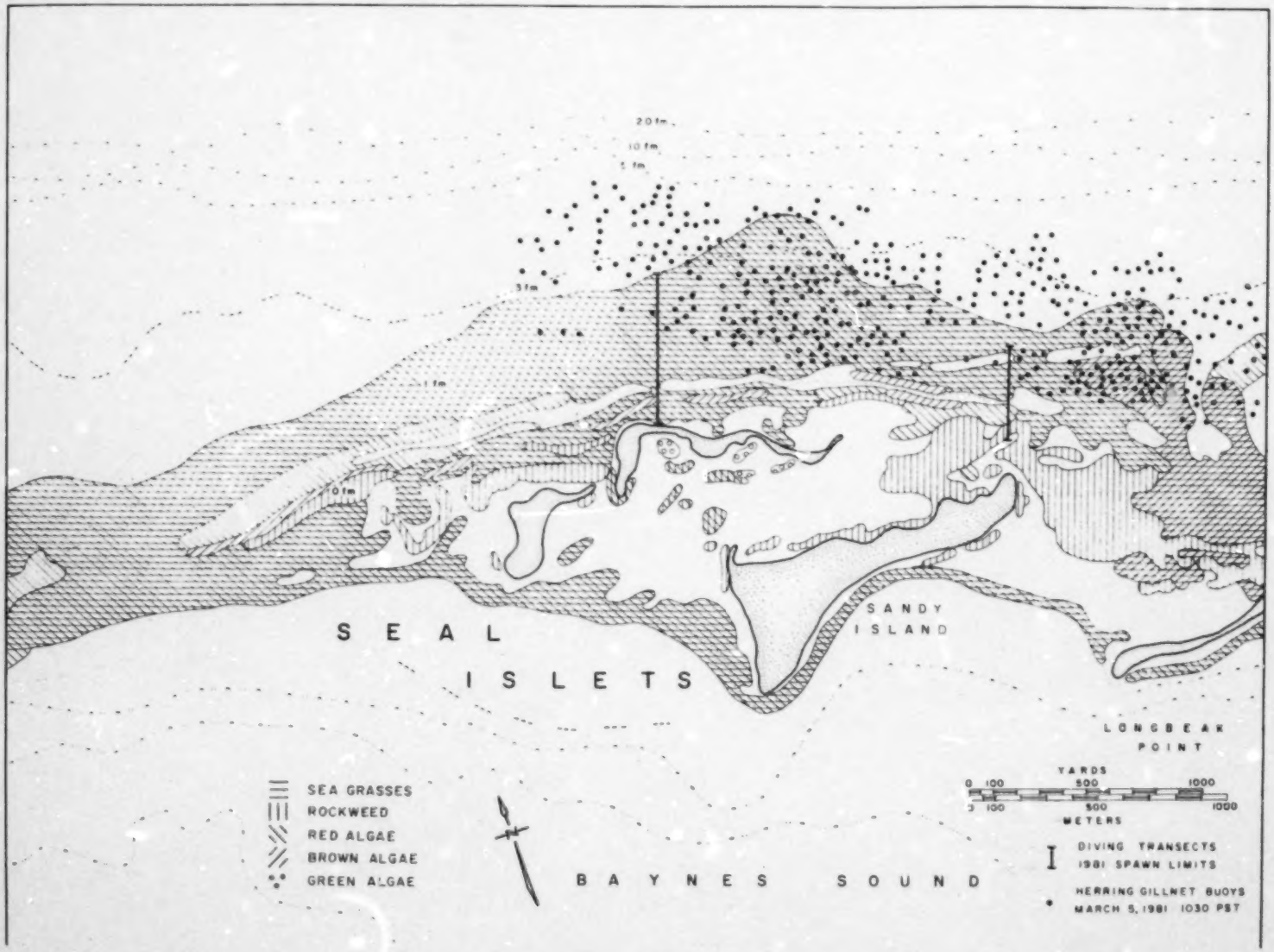


Figure 4. March 5 distribution of gillnets relative to vegetation and spawn near Sandy Island.

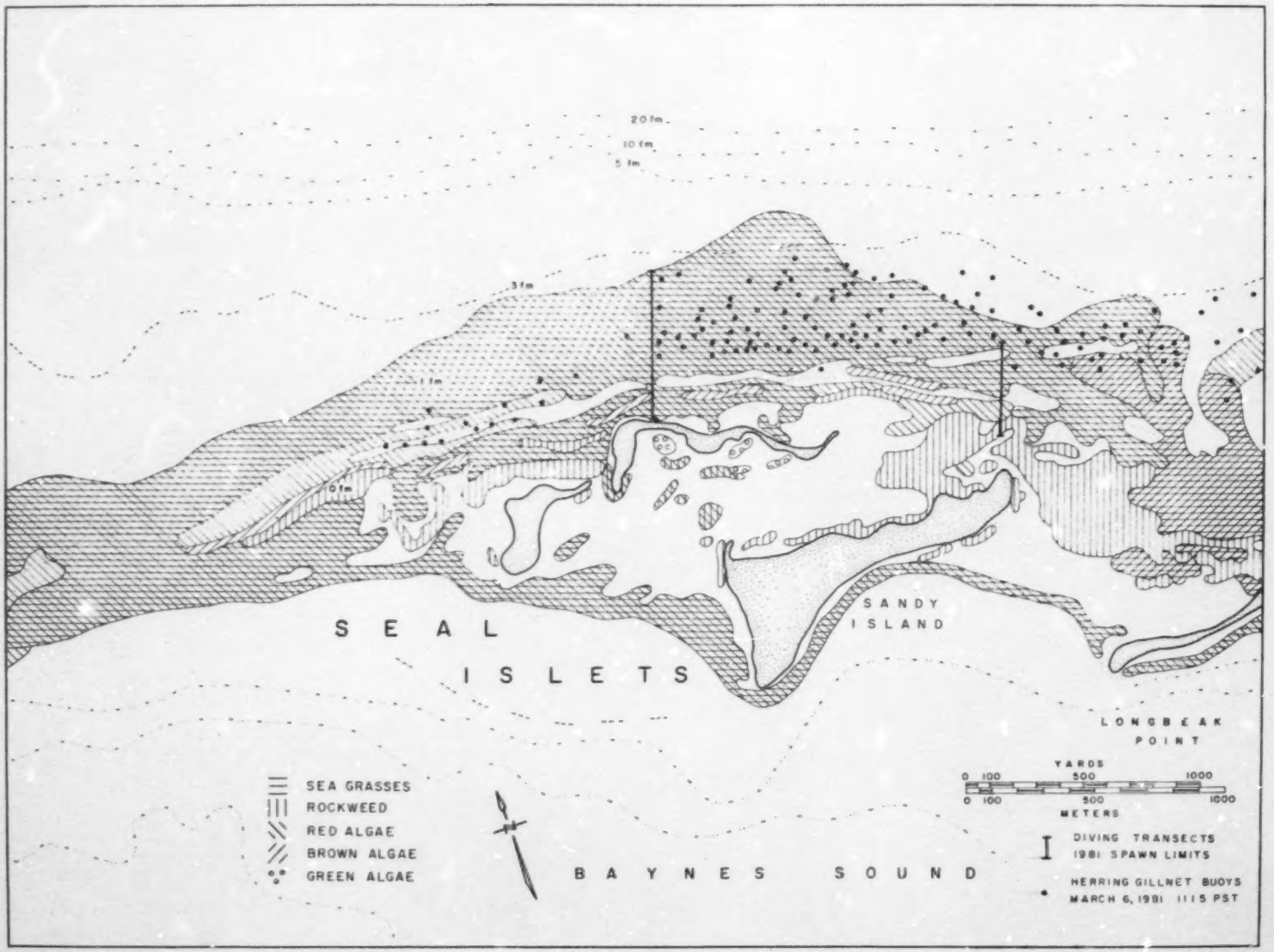


Figure 5. March 6 distribution of gillnets relative to vegetation and spawn near Sandy Island.

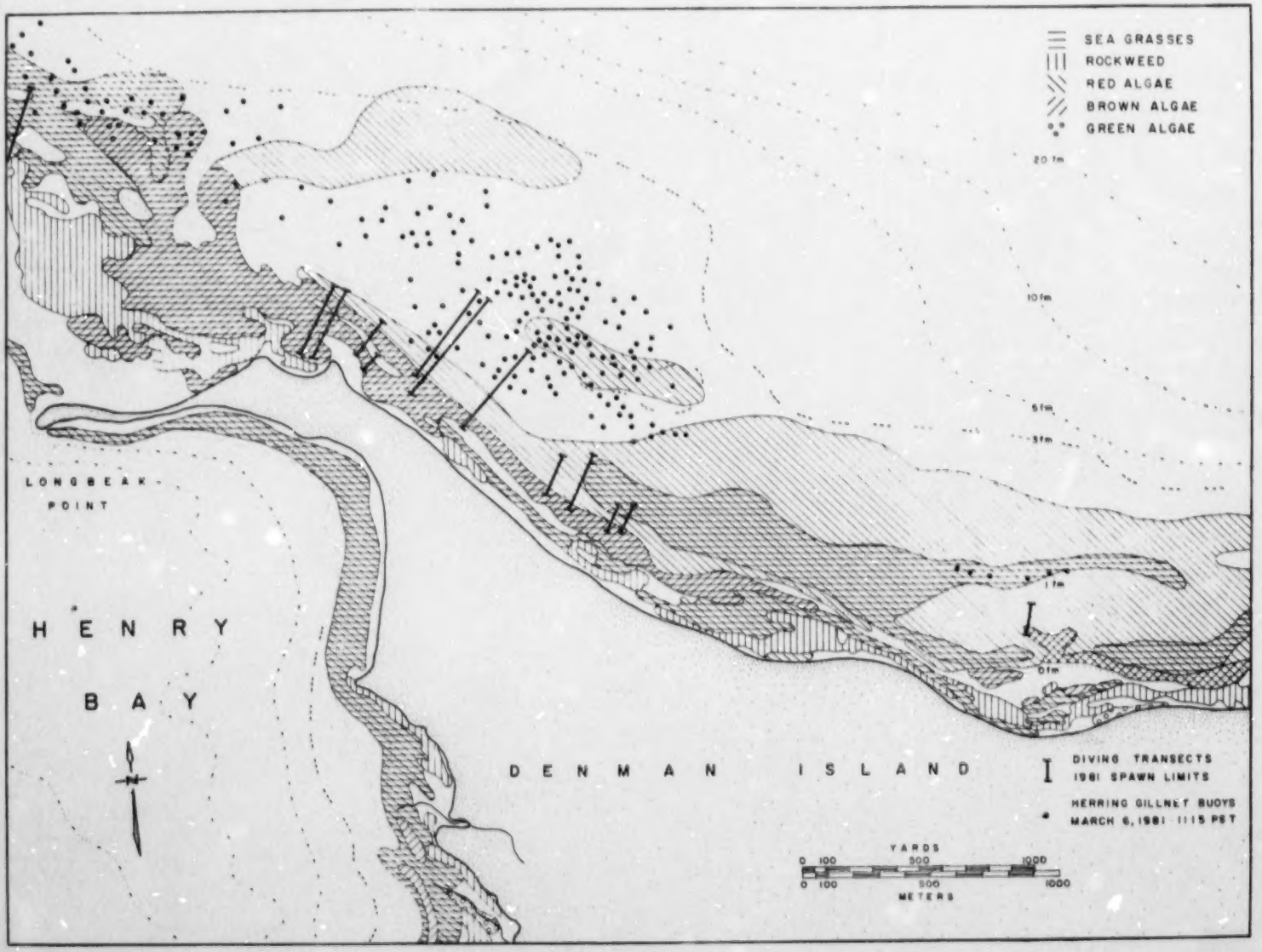


Figure 6. March 5 distribution of gillnets relative to vegetation and spawn in the vicinity of the north end of Denman Island.

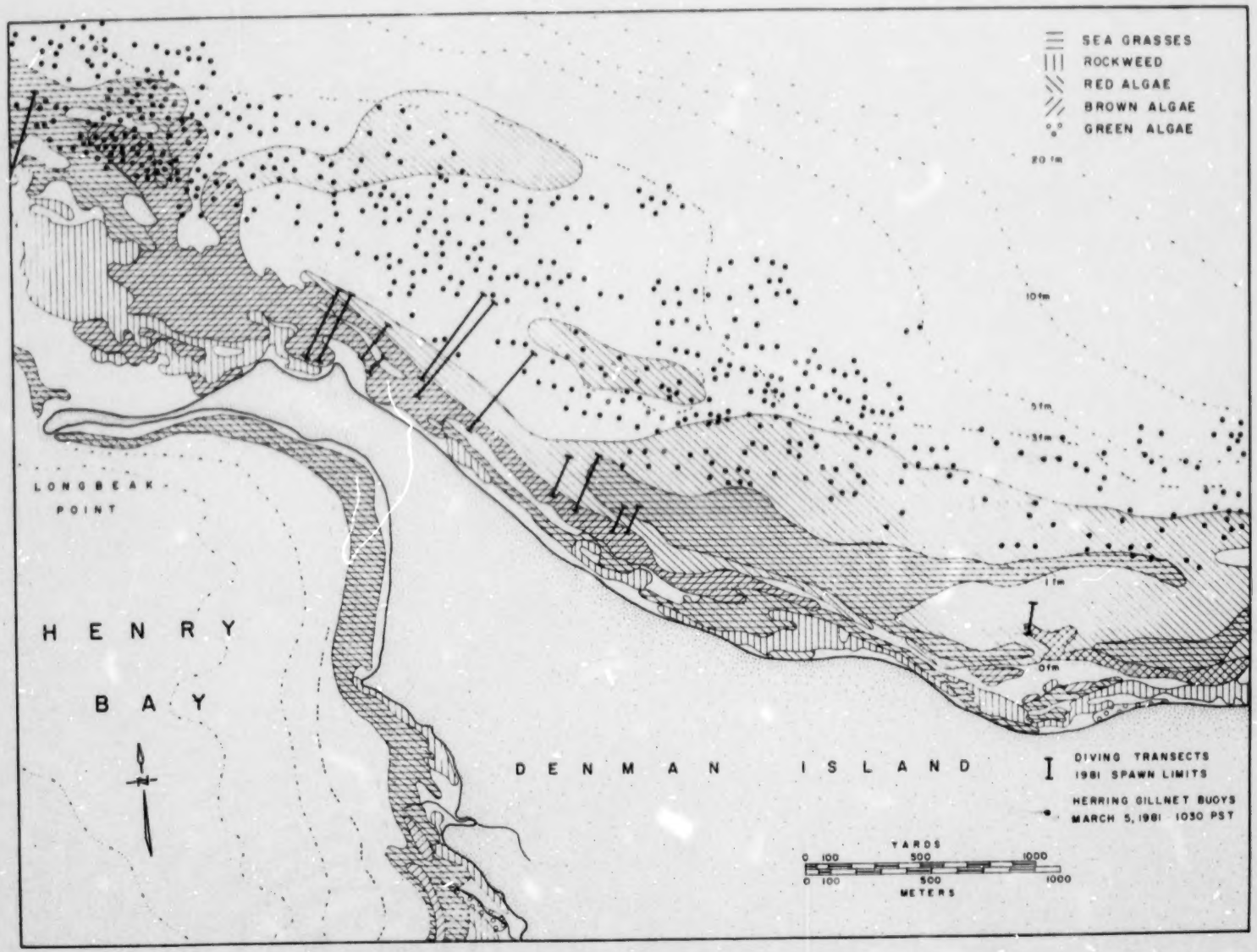


Figure 7. March 6 distribution of gillnets relative to vegetation and spawn in the vicinity of the north of Denman Island.

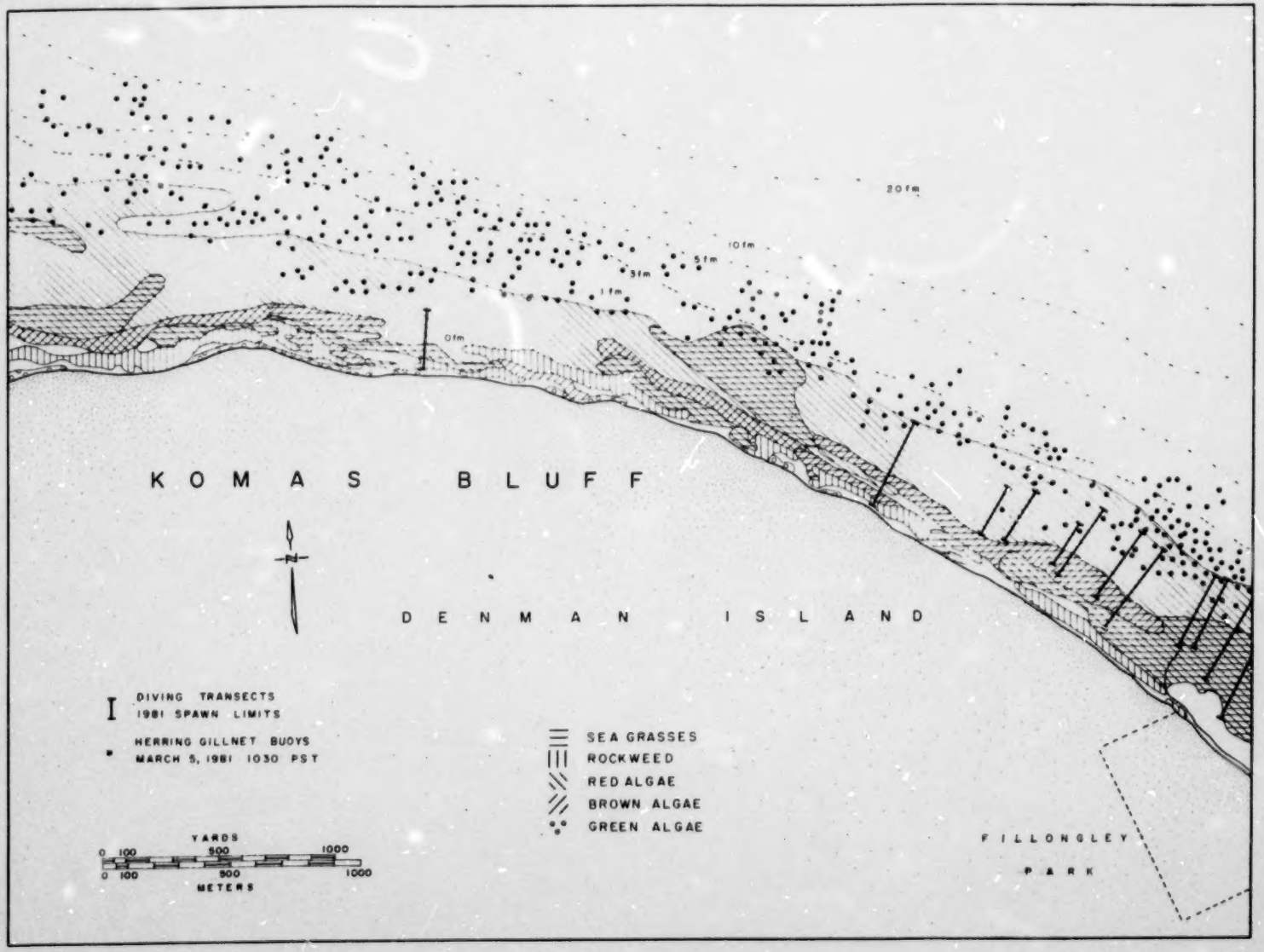


Figure 8. March 5 distribution of gillnets relative to vegetation and spawn in the vicinity of Komas Bluff.

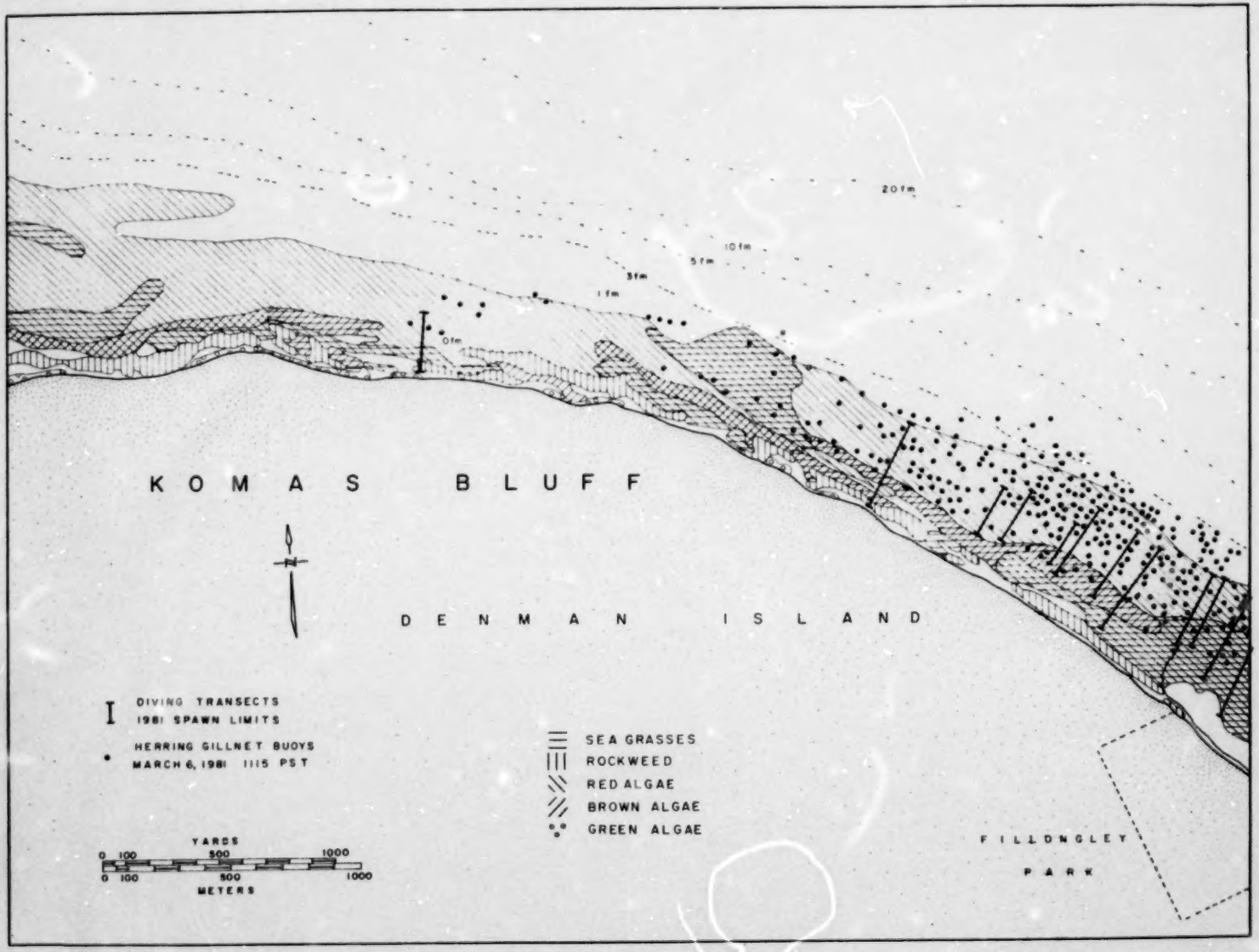


Figure 9. March 6 distribution of gillnets relative to vegetation and spawn in the vicinity of Komas Bluff.

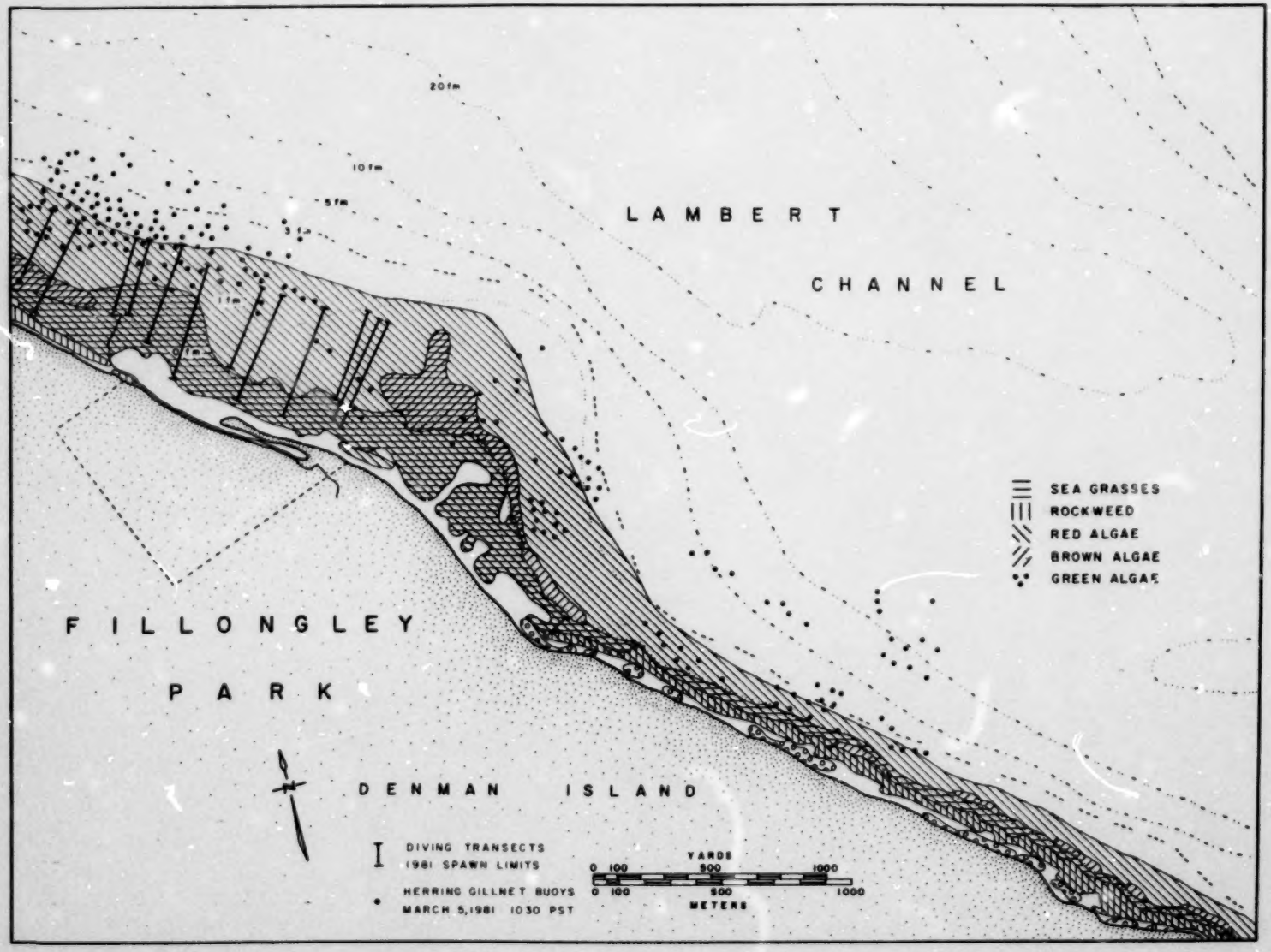


Figure 10. March 5 distribution of gillnets relative to vegetation and spawn in the vicinity of Fillongly Park.

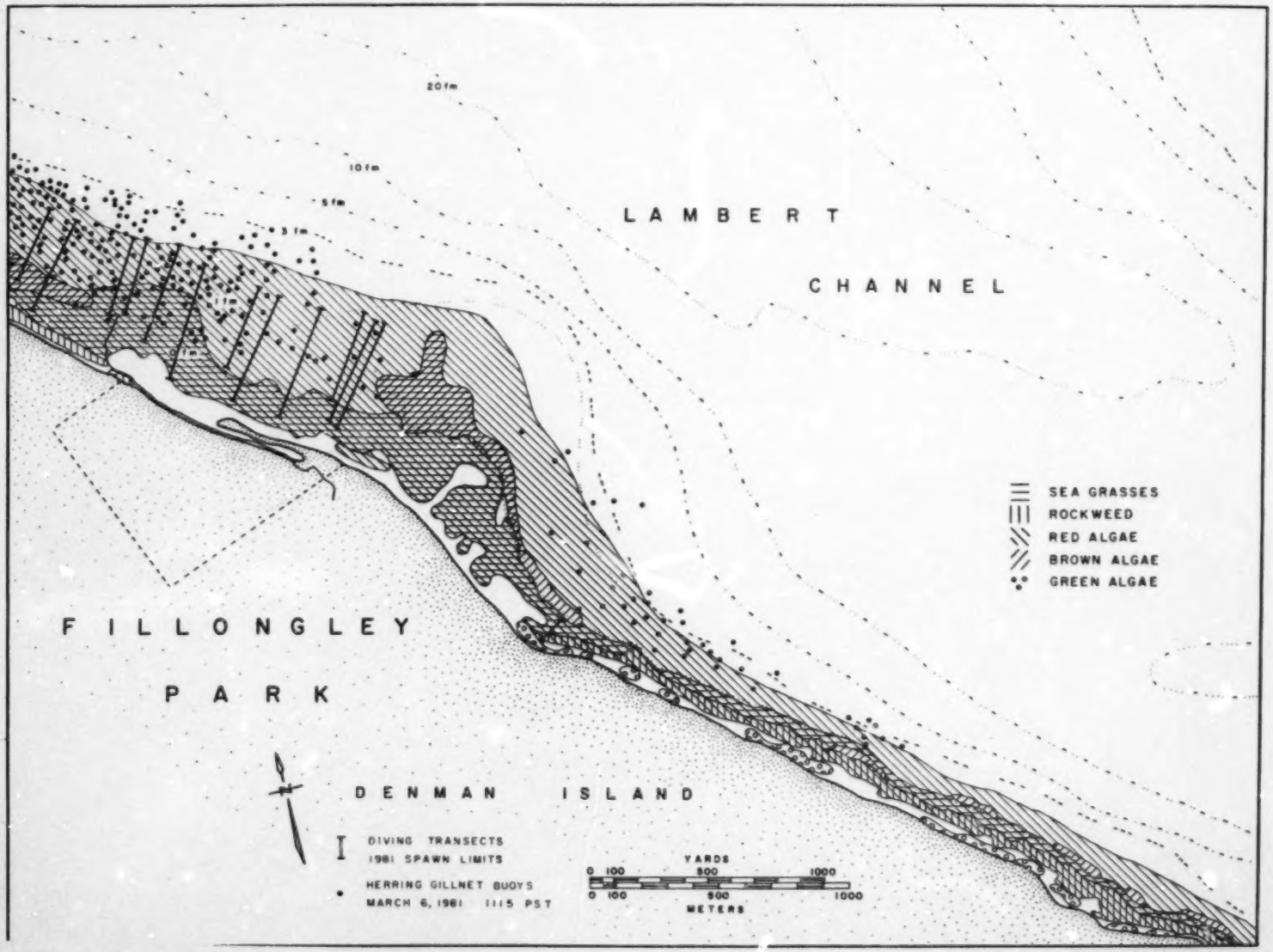


Figure 11. March 6 distribution of gillnets relative to vegetation and spawn in the vicinity of Fillongly Park.

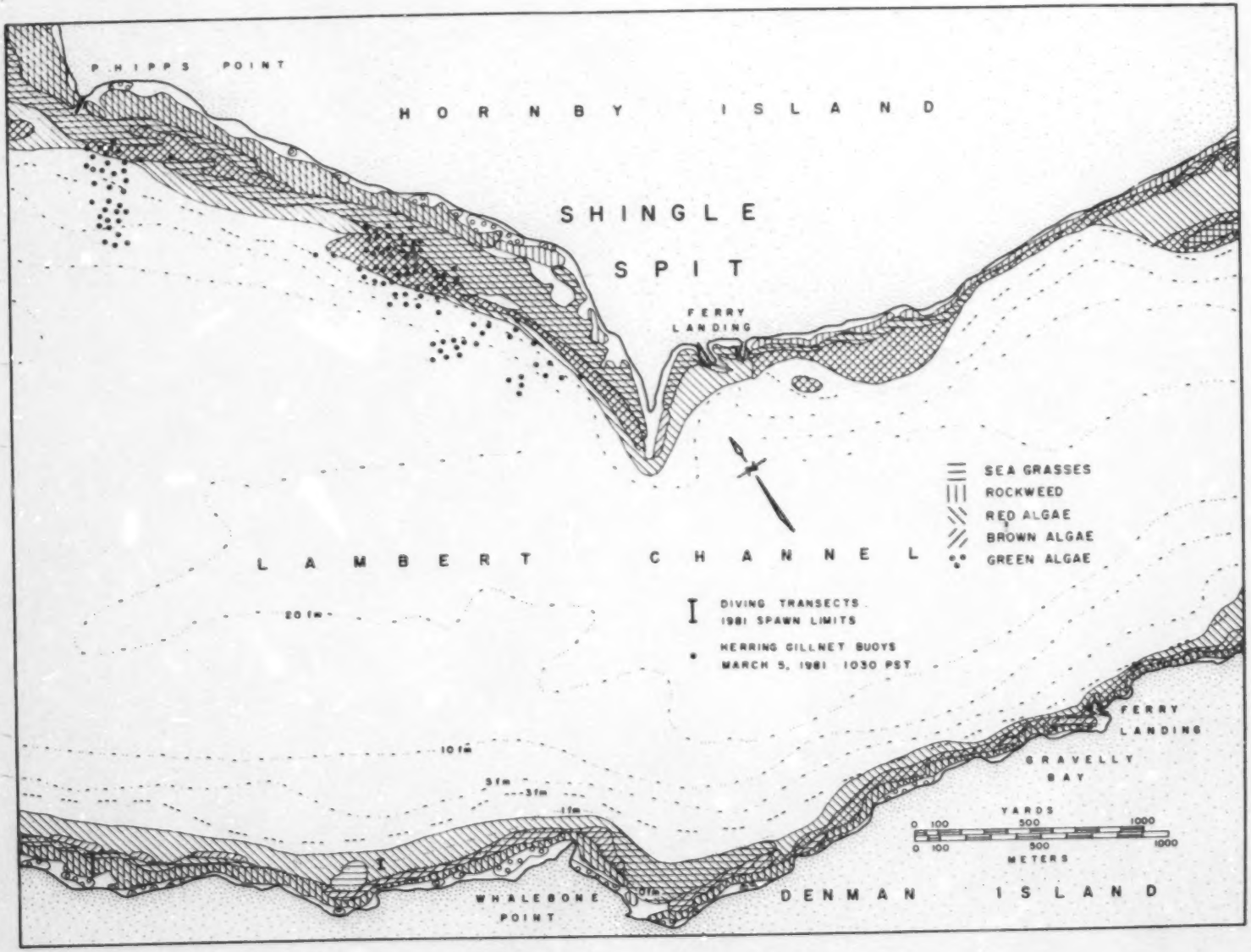


Figure 12. March 5 distribution of gillnets relative to vegetation and spawn near Shingle Spit, Hornby Island.

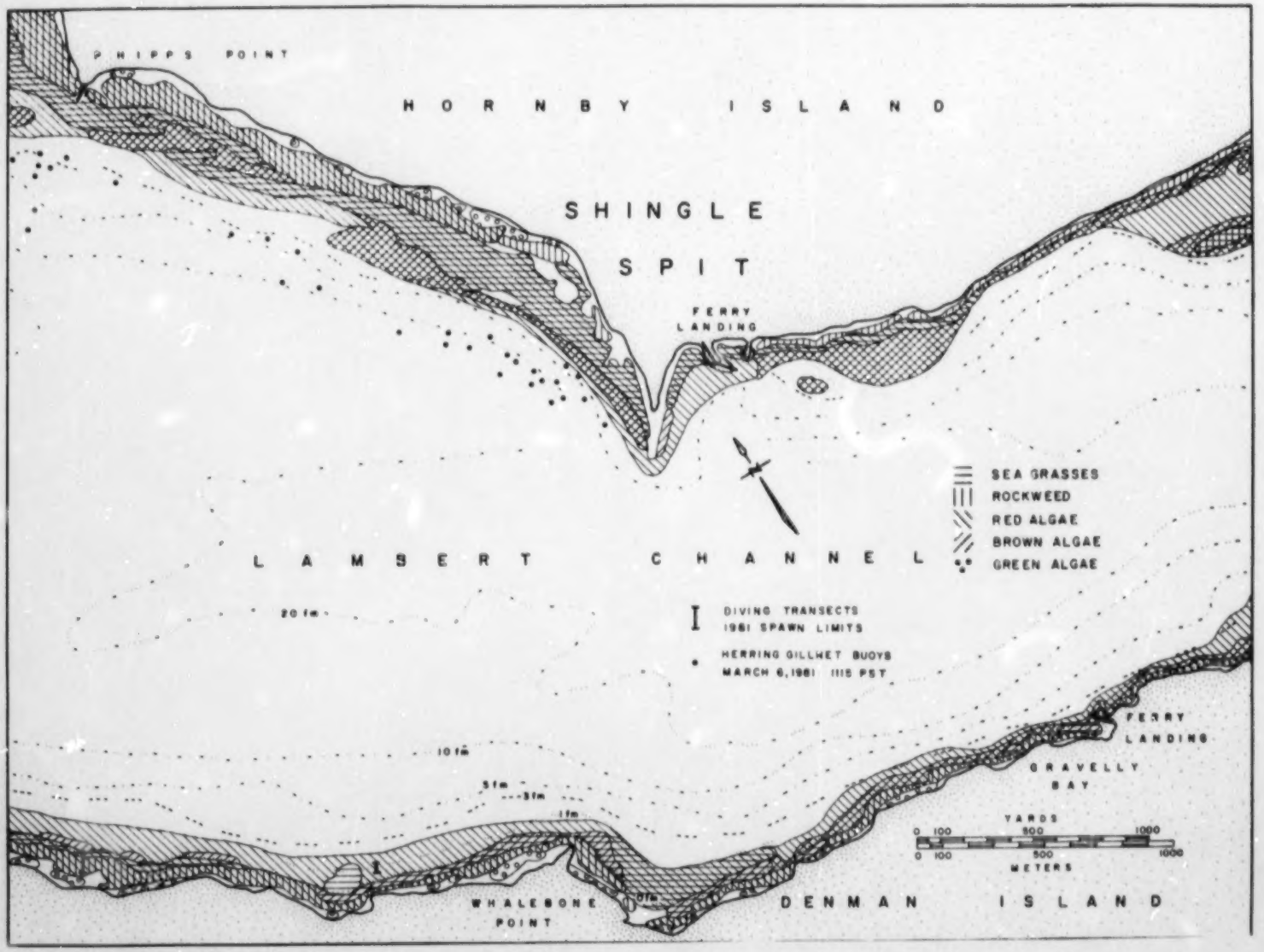


Figure 13. March 6 distribution of gillnets relative to vegetation and spawn near Shingle Spit, Hornby Island.

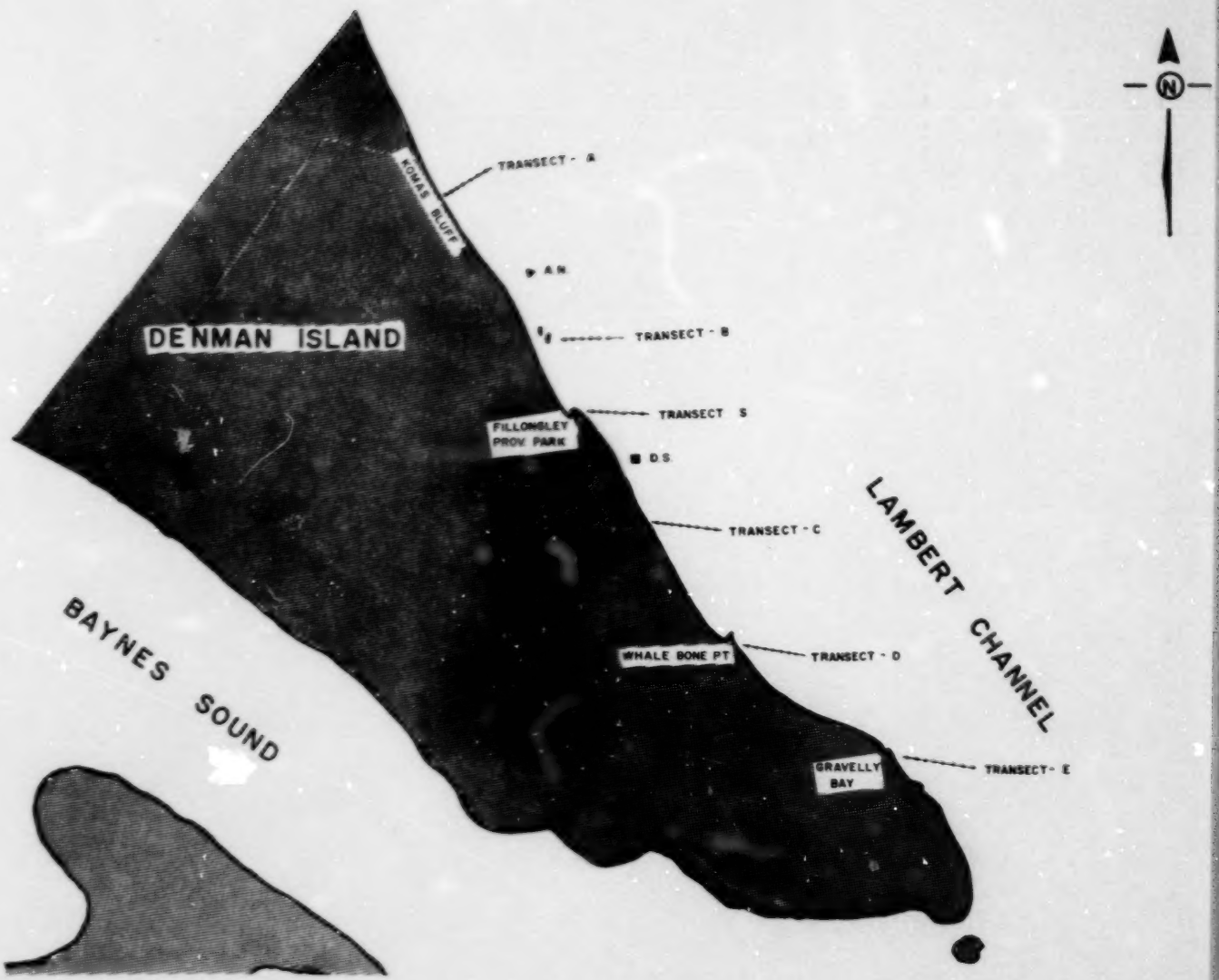


Figure 14. Positions of oceanographic transects, the dumpsite of 500 herring (DS), and the abandoned net (AN).

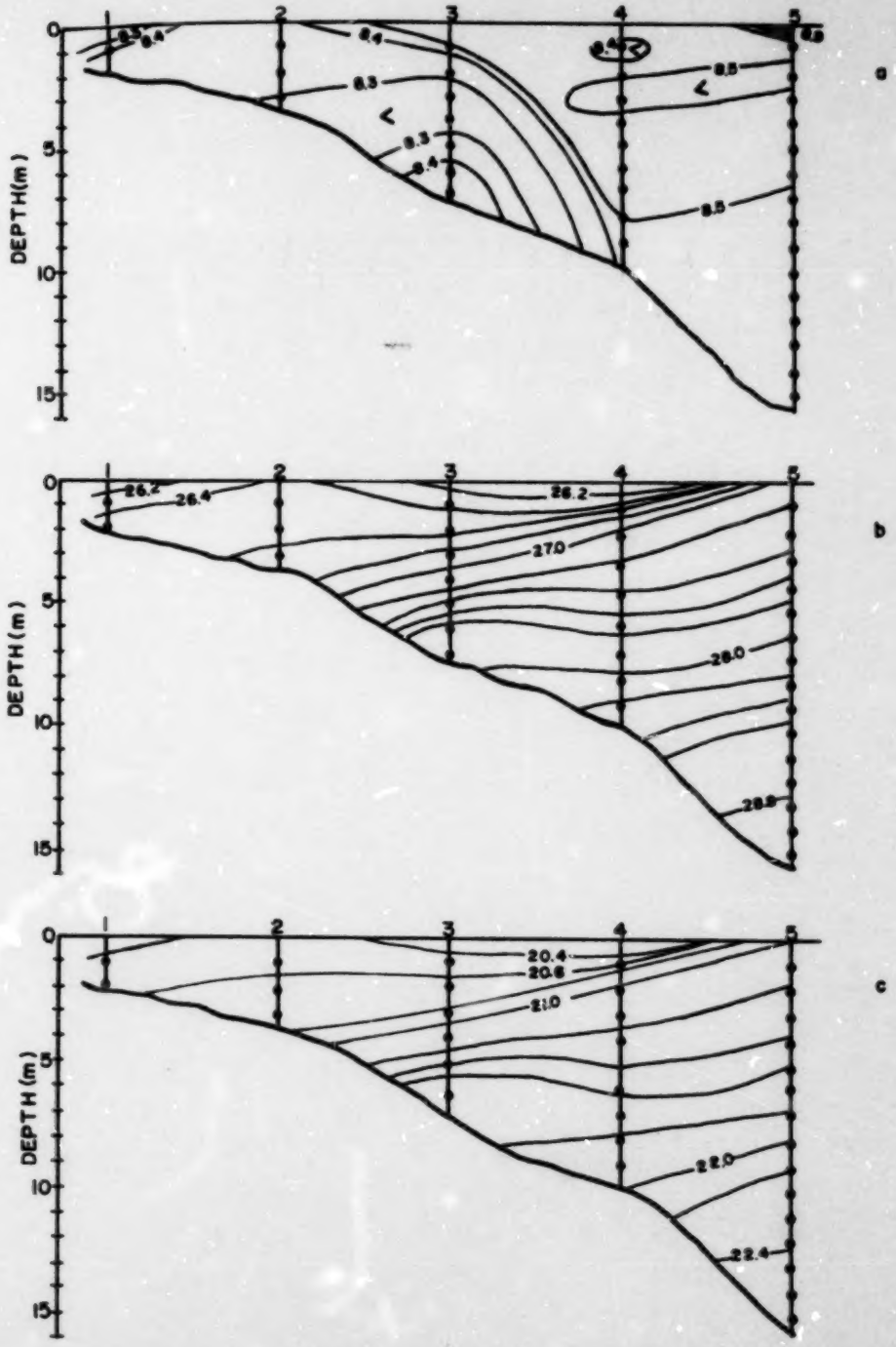


Figure 15a. Profiles of (a) temperature (°C), (b) salinity (°/$_{..}$) and (c) sigma-t along transect A, March 12, 1981.

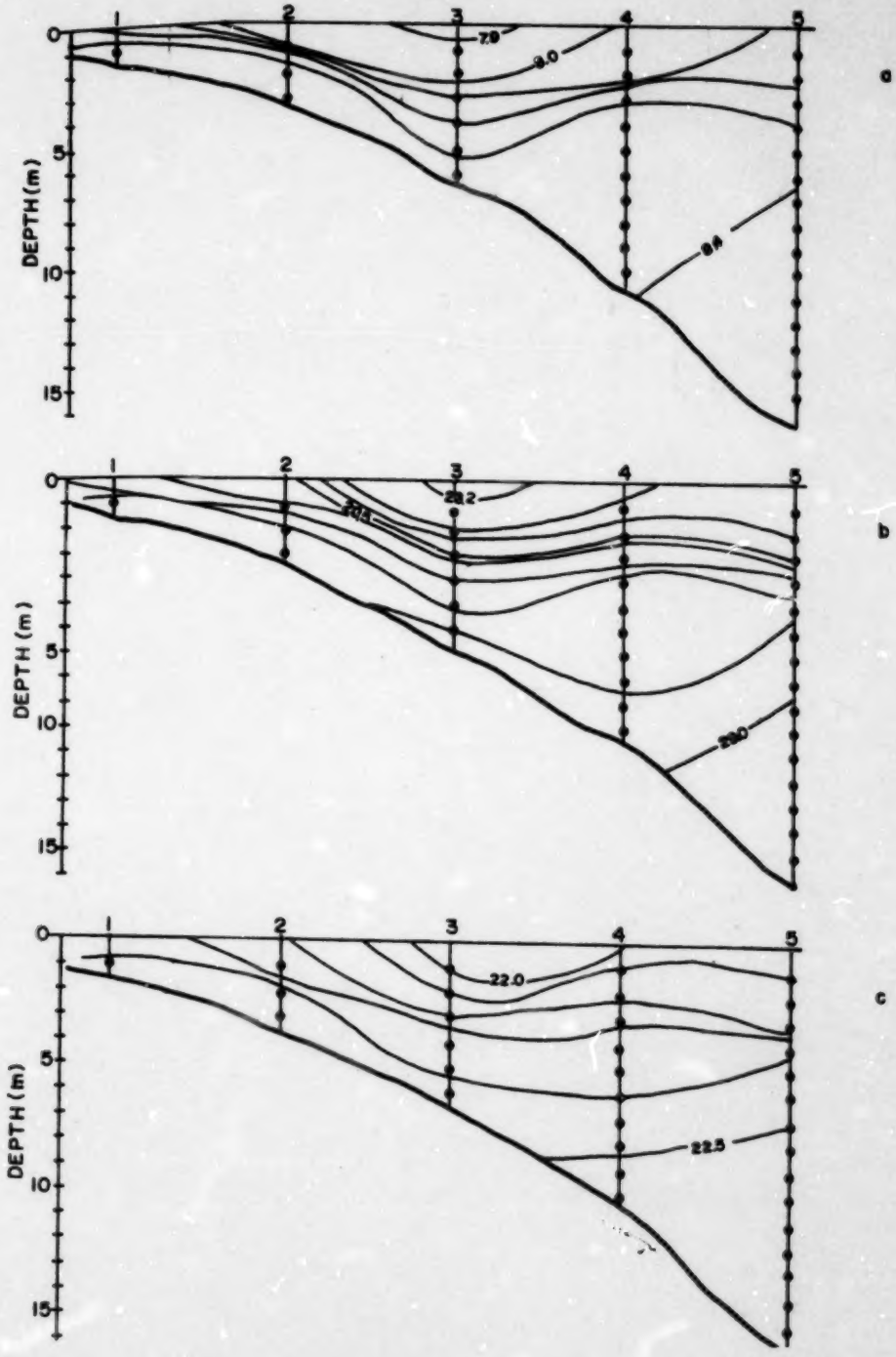


Figure 15b. Profiles of (a) temperature (°C), (b) salinity (°/$_{..}$) and (c) sigma-t along transect B, March 8, 1981.

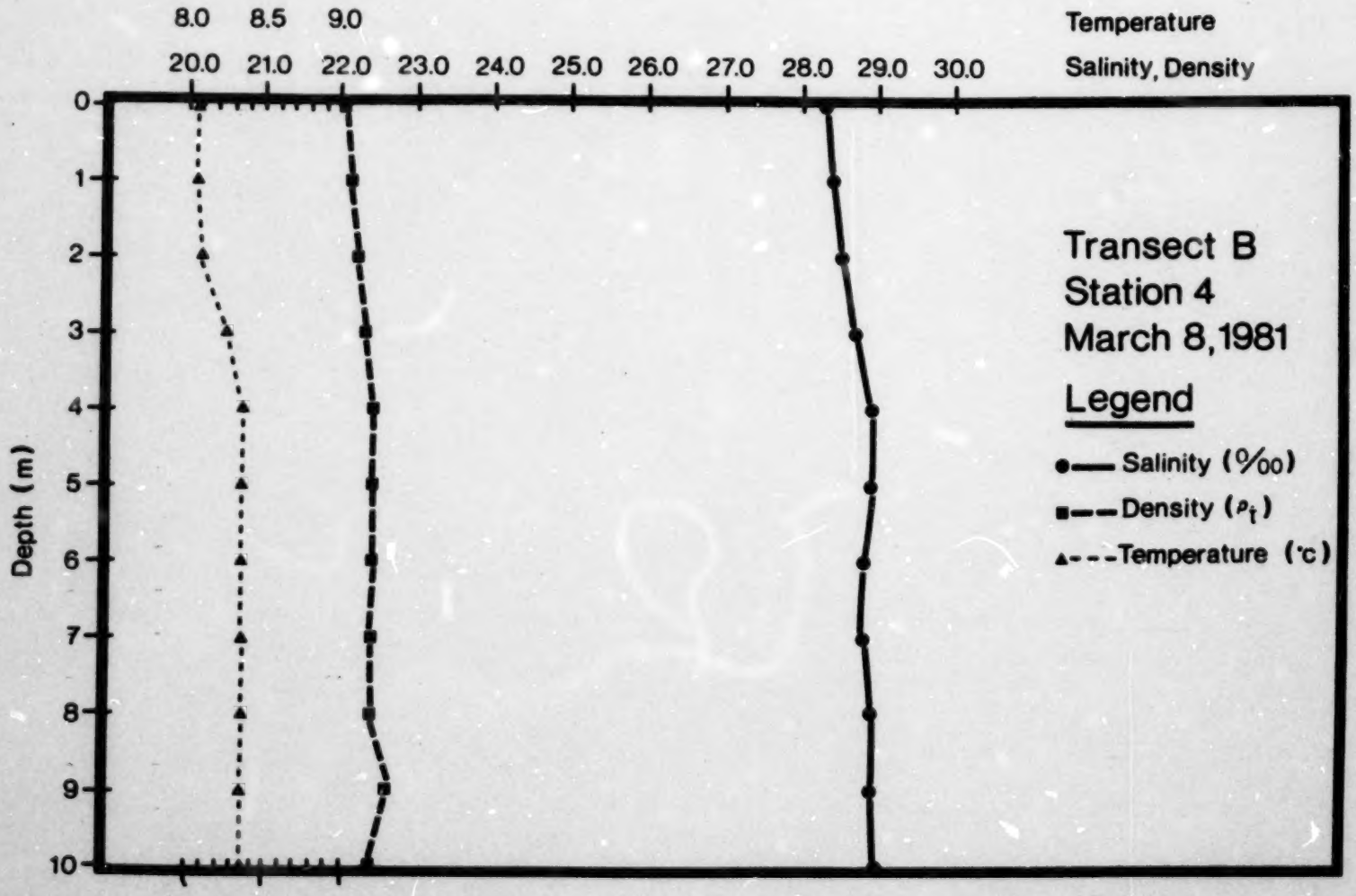


Figure 16. Representative vertical profile of temperature, salinity and density at the study area (transect B , station 4, March 8, 1981, 0945 h).

Figure 17a. Distribution of surface salinity of March 4-5.

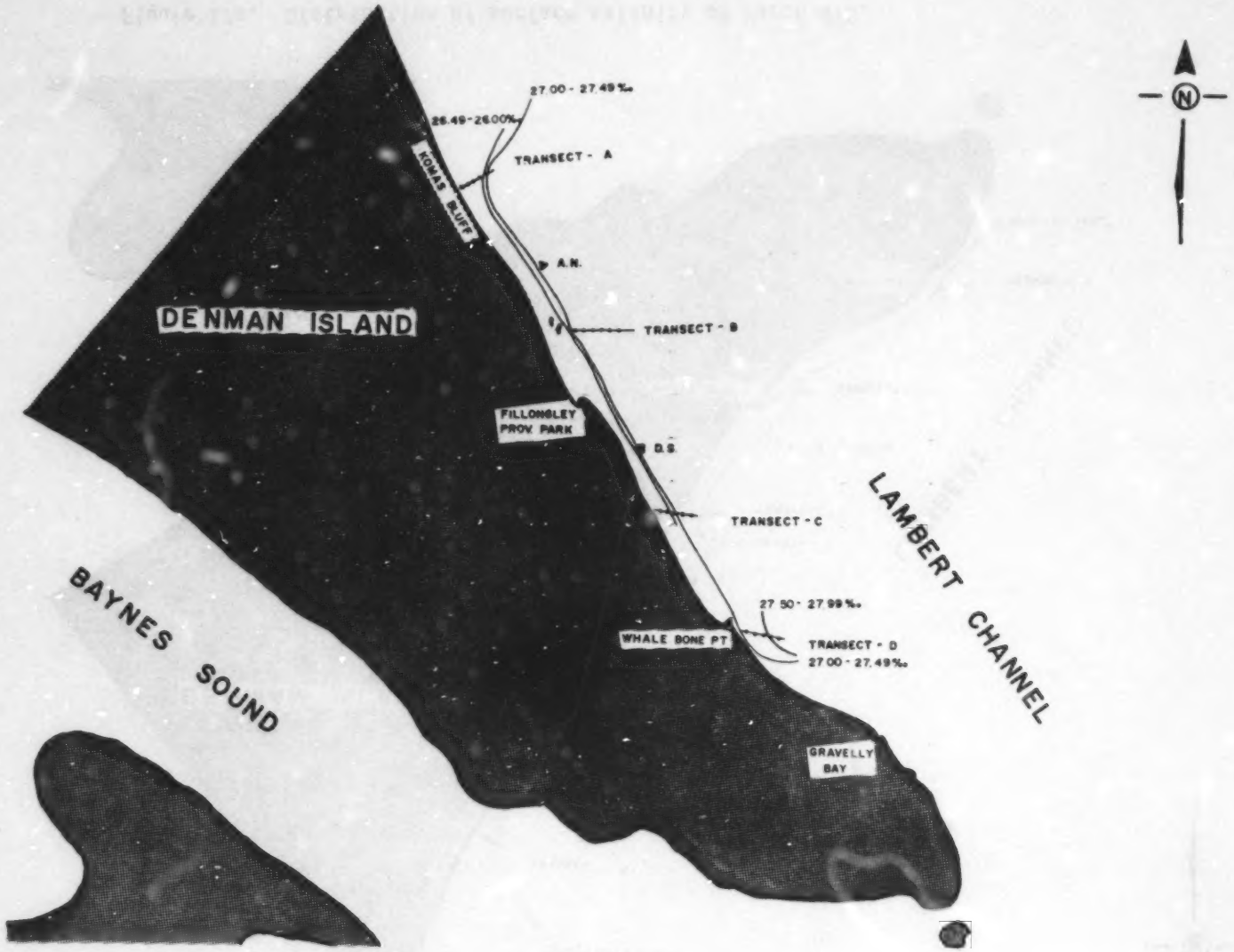


Figure 17b. Distribution of surface salinity on March 12.

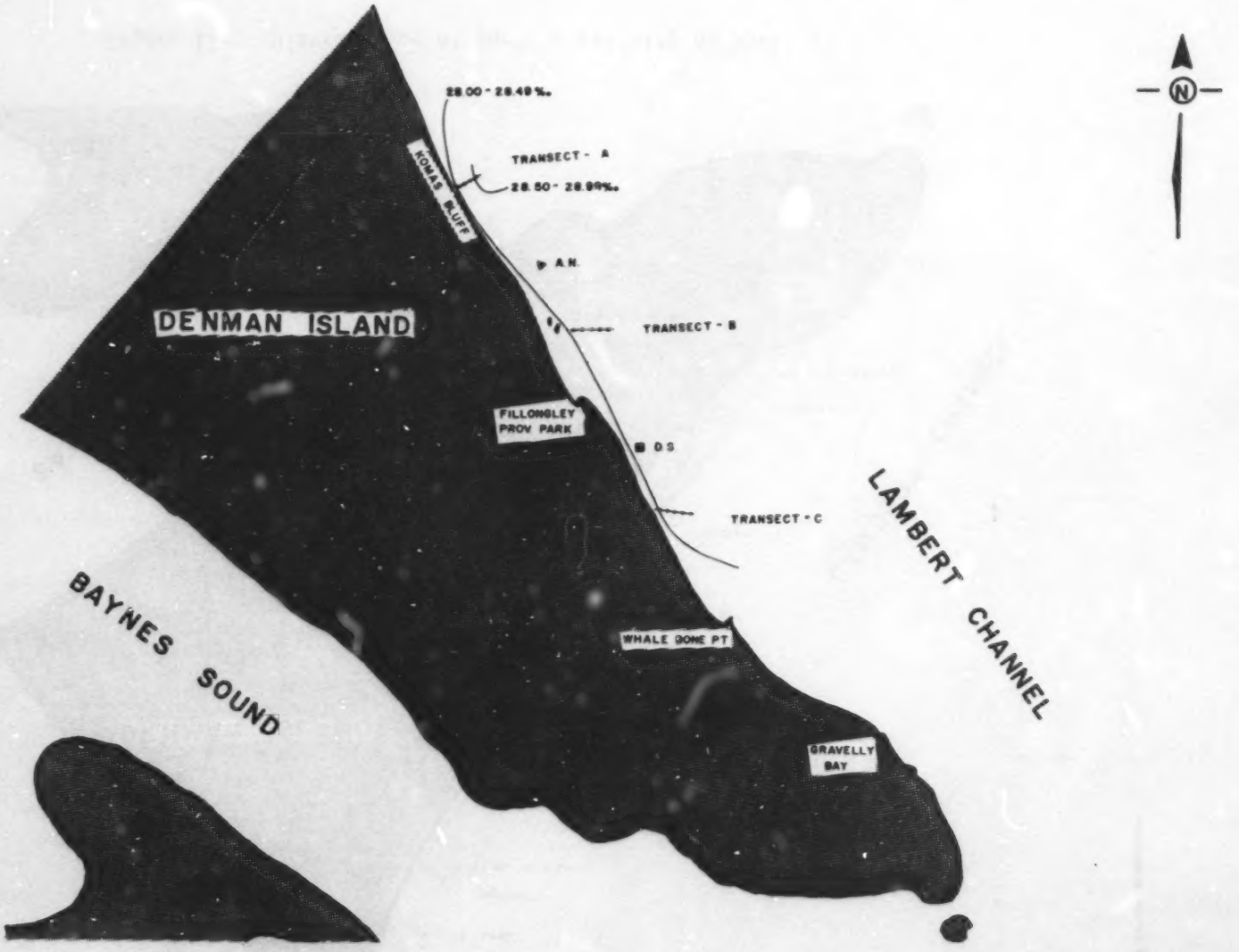


Figure 17c. Distribution of surface salinity on March 26-27.

Figure 17d. Distribution of surface salinity on April 21.

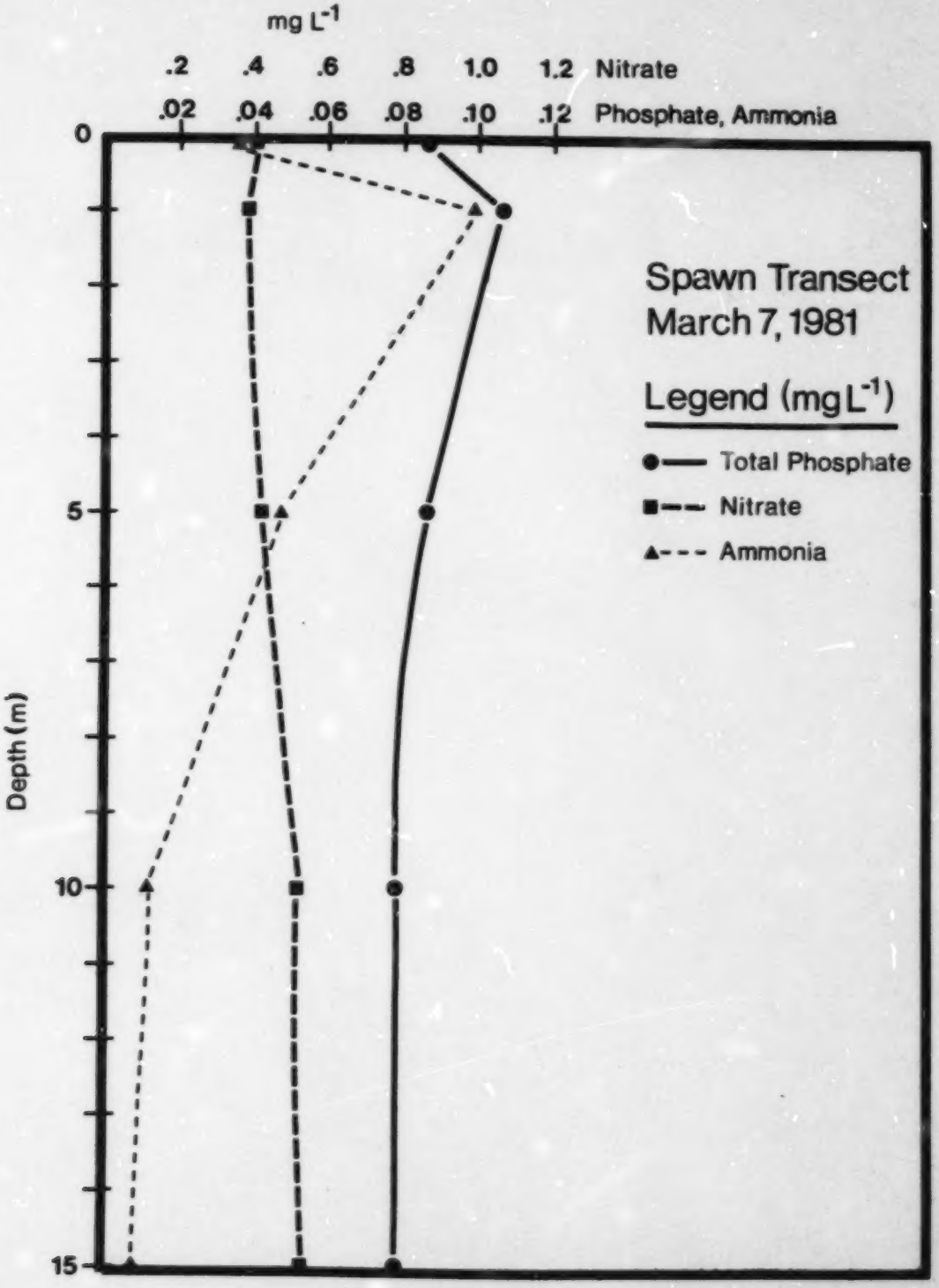
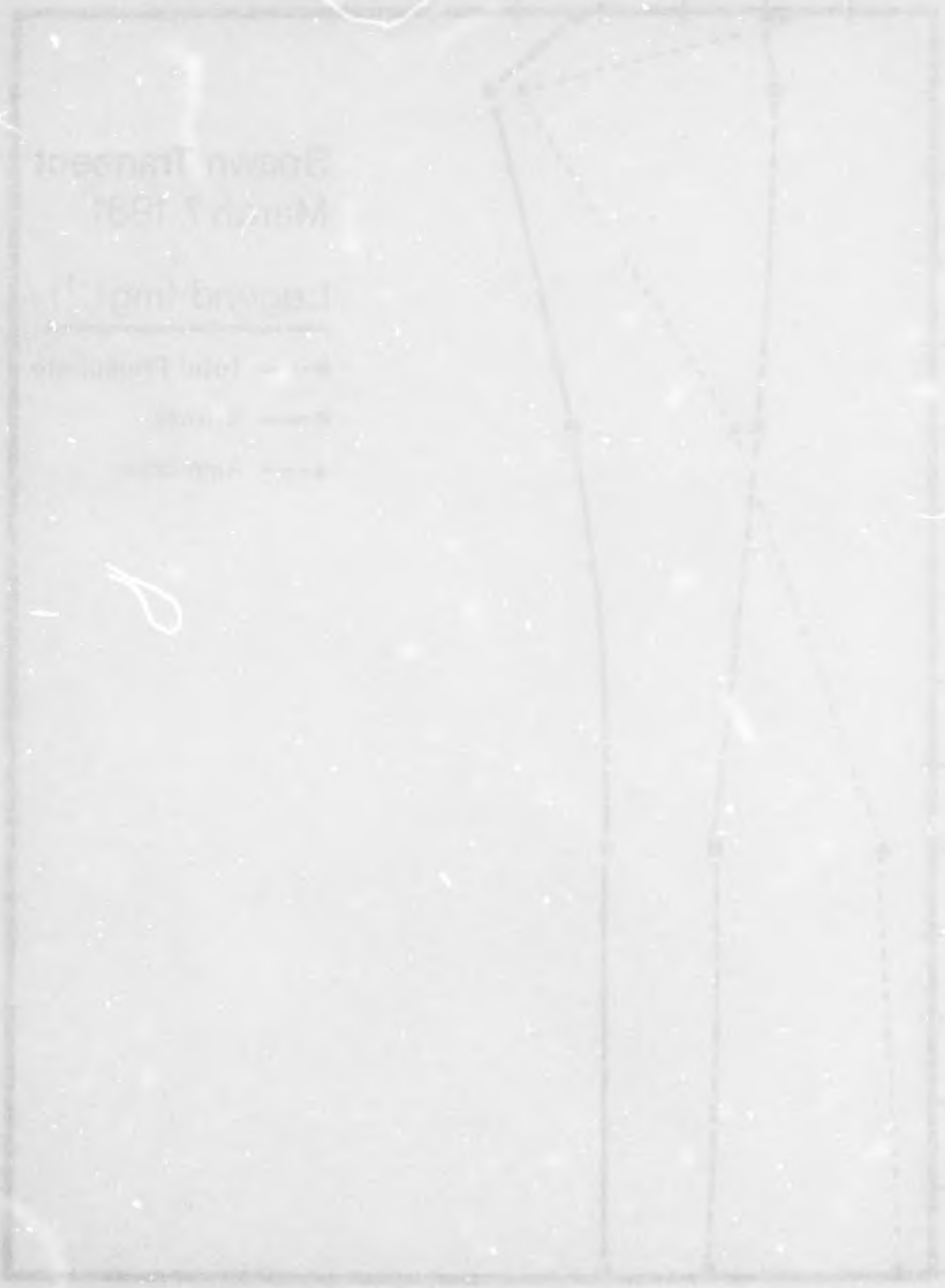


Figure 18. Vertical distribution of total phosphate, nitrate and ammonia on Station 5, Transect 'spawn', March 7, 1981, 1000 h.



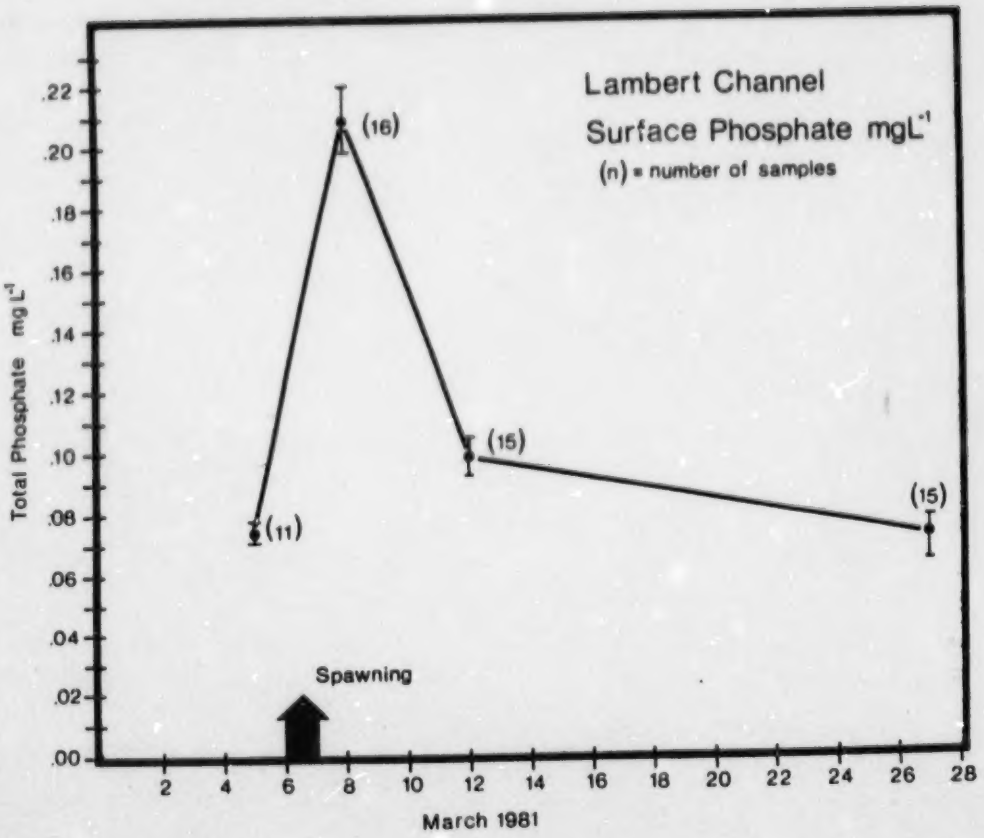


Figure 19. Temporal variation in total phosphate at the surface (mg L^{-1}) in Lambert Channel before, during and after herring spawning. Numbers beside data points indicate the numbers of samples used to calculate mean values, which are shown with standard deviations.

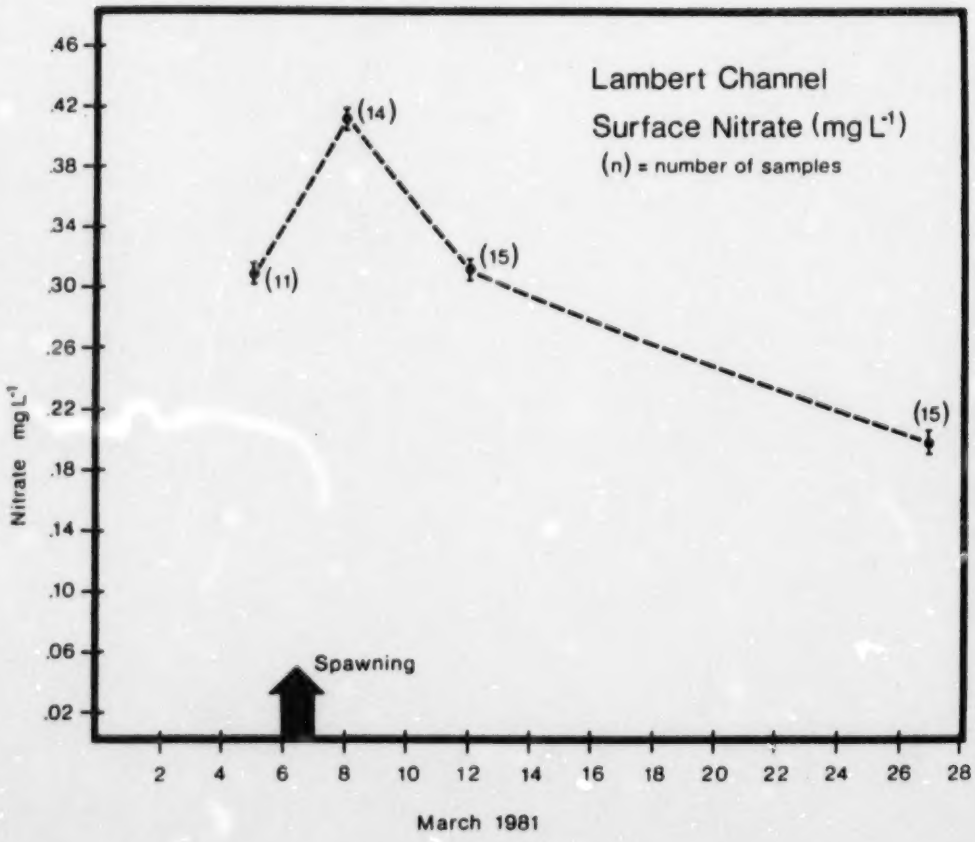


Figure 20. Temporal variation in surface nitrate (mg L^{-1}) in Lambert Channet before, during and after herring spawning. Numbers beside data points indicate the numbers of samples used to calculate mean values, which are shown with standard deviation.